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ABSTRACT

A review of the varied classifications of Recent members of the family Canidae involving morphological, numerical, and reproductive analyses suggests that the taxonomy should be arranged with six monotypic genera (*Chrysocyon*, *Speothos*, *Nyc-*

tereutes, *Cuon*, *Lycaon*, and *Otocyon*), and one polytypic genus, *Canis*, with eight subgenera (*Canis*, *Dusicyon*, *Pseudalopex*, *Lycalopex*, *Cerdocyon*, *Atelocynus*, *Vulpes*, and *Alopex*).

INTRODUCTION

In the past few years reclassifications of the family Canidae have suggested different compositions of the genera. The generic allocations of the canids had been fairly stable for a number of years. A dozen genera and 40 or fewer species were usually recognized.

Most studies followed Simpson's (1945) arrangement of three subfamilies: Caninae, Simocyoninae, and Otocyoninae. In the subfamily Caninae, Simpson had put eight genera: *Canis*, *Alopex*, *Vulpes*, *Fennecus*, *Urocyon*, *Nyctereutes*, *Dusicyon*, and *Chrysocyon*. His subfamily Simocyoninae contained the genera *Speothos*, *Cuon*, and *Lycaon*. *Otocyon* was the sole representative of the subfamily Otocyoninae.

Until 1969, subsequent compilations and classifications had, in general, continued to use these genera, the most consistent change being

the recognition of *Cerdocyon* and *Atelocynus* as valid genera. They had been included in *Dusicyon* by Simpson (1945). Stains (1967, 1975) recognized *Dasycyon*, a genus named by Krumbiegel (1949, 1953).

Lately, the South American canids have been studied by Langguth (1969, 1975), and the entire family was subjected to a numerical analysis by Clutton-Brock, Corbet, and Hills (1976). The conclusions of these studies are different, and in attempting to recommend taxonomic changes that seemed warranted on the basis of intergeneric hybridization, I (Van Gelder, 1977) found it necessary to attempt a consistent arrangement of the genera that differs from that of Langguth (1975) and Clutton-Brock, Corbet, and Hills (1976) or any other current classification. The present paper is an analysis of these different classifications.

¹Curator, Department of Mammalogy, the American Museum of Natural History.

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DISCUSSION

Other than the genera that Simpson (1945) included in the Caninae, there has been little dispute concerning the content of the genera of canids that Simpson had placed in the Simocyoninae and Otocyoninae. The alliance of *Speothos*, *Cuon*, and *Lycaon* in a single subfamily had been questioned (Pocock, 1941; Ellerman and Morrison-Scott, 1951; Todd, 1970), and Simpson himself (1945) admitted that it was a heterogeneous group. Clutton-Brock, Corbet, and Hills (1976) found that subfamilial separations in the Canidae were not warranted. They concluded that each of these genera represented a monotypic, highly specialized entity whose relationship to the others was distant, although perhaps closer to one another than to those genera that were usually placed in the subfamily Caninae. Similarly, Clutton-Brock, Corbet, and Hills did not recognize the subfamily Otocyoninae for *Otocyon*. The distinction of each of these four genera that were formerly split off from the Caninae is unquestioned. There seems also to be no question about the recognition of *Nyctereutes* as a distinctive canid genus, although Frechkop (1959) proposed that it belonged with the procyonids. *Chrysocyon* also is universally recognized as a clearcut genus. It is the other genera within the Caninae that have received most of the current attention and rearrangement that have resulted in the unequal classifications.

For clarity in the following discussion, I must define the extent of the genera that I shall mention. For these purposes I follow the listings of Stains (1967, 1975):

Alopex Kaup, 1829. One species: *A. lagopus*.
Atelocynus Cabrera, 1940. One species: *A. microtis*.

Canis Linnaeus, 1758. Nine species: *C. adustus*, *aureus*, *mesomelas*, *dingo*, *familiaris*, *latrans*, *lupus*, *niger*, and *simensis*.

Cerdocyon H. Smith, 1839. One species: *C. thous*.

Dusicyon H. Smith, 1839. Nine species: *D. australis*, *culpaesus*, *culpaesolus*, *griseus*, *fulvipes*, *gymnocercus*, *sechurae*, *vetulus*, and *inca*.

Fennecus Desmarest, 1804. One species: *F. zerda*.

Urocyon Baird, 1858. Two species: *U. cinereoargenteus*, and *littoralis*.

Vulpes Bowdich, 1821. Ten species: *V. bengalensis*, *cana*, *chama*, *corsac*, *ferrilata*, *macrotis*, *pallida*, *rueppelli*, *velox*, and *vulpes*.

Additional clarification of these genera and species can be made and, in fact, Stains evidently made some changes between his 1967 and 1975 listings. *Canis dingo* is now generally regarded as a distinctive feral domestic dog. *Canis familiaris* is used for domestic dogs, although taxonomically it should probably be synonymous with *Canis lupus*. In 1975 Stains had dropped *Dusicyon culpaesolus*, evidently following Langguth (1967). He did not regard *Dusicyon fulvipes* as specifically distinct from *D. griseus*. *Dusicyon inca* also was no longer recognized by Stains (1975), again following Langguth (1967). Stains listed only six species of *Dusicyon* in 1975: *D. australis*, *culpaesus*, *griseus*, *gymnocercus*, *sechurae*, and *vetulus*. Stains (1975) listed *Urocyon littoralis* in his account of *U. cinereoargenteus*, pointing out that these insular populations are regarded by some as subspecies of *U. cinereoargenteus*, and by others as subspecies of a separable species, *U. littoralis*.

Stains (1967, 1975) persisted in recognizing *Dasycyon hagenbecki*, known only from a single skin. Cabrera (1958) and Hershkovitz (1961) have indicated that this genus and species is most probably a domestic dog.

For the South American canids, in addition to *Urocyon*, *Chrysocyon*, and *Speothos*, Cabrera (1958) recognized three genera: *Dusicyon*, *Atelocynus*, and *Cerdocyon*. Simpson (1945) had put these in the genus *Dusicyon* and followed Osgood (1934) in subdividing it into three subgenera: *Dusicyon* (including *Pseudalopex*), *Cerdocyon* (including *Atelocynus*), and *Lycalopex*. Cabrera (1958) divided his genus

Dusicyon into two subgenera: *Dusicyon*, and *Lycalopex*. The latter contained only *Dusicyon vetulus*.

Langguth (1969) arranged the South American canids at quite different levels. His classification, which excluded *Urocyon*, had *Chrysocyon*, *Dusicyon*, and *Cerdocyon* as genera. The first two were monotypic. *Dusicyon* was divided into two subgenera, *Dusicyon* for *D. australis* alone, and *Pseudalopex* for *D. culpaeus*, *gymnocercus*, and *griseus*. His genus *Cerdocyon* was divided into three subgenera: *Cerdocyon*, *Atelocynus*, and *Speothos*.

Subsequently (1975), Langguth changed his classification of the South American canines. He gave generic rank to the differentiated kinds, *Cerdocyon*, *Speothos*, *Lycalopex*, and *Atelocynus*, and he placed the Patagonian canids, formerly called *Dusicyon*, in the genus *Canis*. He recognized the subgenus *Dusicyon* for the Falkland wolf, *C. australis* only, and put the other species (*culpaeus*, *gymnocercus*, and *sechurae*), in a second subgenus of *Canis*, *Pseudalopex*.

At the end of 1975, the species in the genus *Canis* included *C. adustus*, *aureus*, *mesomelas*, *familiaris*, *latrans*, *lupus*, and *niger*, in the subgenus *Canis*; *C. simensis* in the subgenus *Simenia* (Ellerman, Morrison-Scott, and Hayman, 1953); *C. australis* in the subgenus *Dusicyon*; and *C. culpaeus*, *gymnocercus*, *griseus*; and *sechurae* in the subgenus *Pseudalopex*.

In 1976 Clutton-Brock, Corbet, and Hills published a classification based on a numerical analysis of the family Canidae. For the South American canids they recognized only *Chrysocyon* and *Speothos* as monotypic genera, put *Urocyon* in *Vulpes*, and included all the other South American canids in the genus *Dusicyon*, more or less returning these species to the arrangement (without subgenera) of Simpson in 1945.

Excluding the placement of *Urocyon* in *Vulpes* by Clutton-Brock, Corbet, and Hills (1976), which was a novel proposal—discussed later in the present paper—the alternatives for the classification of South American canids at present are:

	Clutton-Brock, Corbet, and Hills, 1976	Langguth, 1975
<i>culpaeus</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Canis</i> , subgenus <i>Pseudalopex</i>
<i>culpaolus</i>	possibly conspecific with <i>culpaeus</i> , but needs study	skin is <i>culpaeus</i> , skull is <i>gymno-</i> <i>cercus</i> ; mismatch (Langguth, 1967)
<i>gymnocercus</i>	possibly conspecific with <i>culpaeus</i> , but needs study	valid species, placed in the genus <i>Canis</i> , subgenus <i>Pseudalopex</i>
<i>inca</i>	possibly conspecific with <i>culpaeus</i> , but needs study	skin is <i>gymnocercus</i> skull is <i>culpaeus</i> ; mismatch (Langguth, 1967)
<i>griseus</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Canis</i> , subgenus <i>Pseudalopex</i>
<i>fulvipes</i>	possibly conspecific with <i>griseus</i> , but needs more study	conspecific with <i>griseus</i> , valid as a subspecies
<i>sechurae</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Canis</i> , subgenus <i>Pseudalopex</i>
<i>vetulus</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Lycalopex</i>
<i>thous</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Cerdocyon</i>
<i>microtis</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Atelocynus</i>
<i>australis</i>	valid species, placed in the genus <i>Dusicyon</i>	valid species, placed in the genus <i>Canis</i> , subgenus <i>Dusicyon</i>
<i>brachyurus</i>	valid species, placed in the genus <i>Chrysocyon</i>	valid species, placed in the genus <i>Chrysocyon</i>
<i>venaticus</i>	valid species, placed in the genus <i>Speothos</i>	valid species, placed in the genus <i>Speothos</i>

Langguth's reason for assigning the Patagonian canids to *Canis* was based on the high degree of morphological similarity, especially of the skulls. He pointed out the difficulty of distinguishing, for example, a skull of *Canis adustus* from *Canis (Pseudalopex) culpaeus*. He believed that the degree of difference between these two species did not warrant generic separation. Both *Canis* and the former genus *Dusicyon* have maintained what he called a basic, generalized canid pattern (Langguth 1975).

Although Clutton-Brock, Corbet, and Hills (1976) came to a different taxonomic conclusion from that of Langguth, they essentially confirmed Langguth's merging of *Dusicyon* with *Canis*. In their tables of systematic position of various species (percentage similarity to "near neighbours") they show, for example, that *Dusicyon australis* is more similar to *Canis familiaris* than is *Canis aureus*, that *Dusicyon gymnocercus* is more similar to *Canis mesomelas* than that jackal is to *Canis adustus* or *C. aureus*. In the case of *Canis simensis*, Clutton-Brock, Corbet, and Hills showed that the five nearest neighbors are *Dusicyon*.

In their table I of the mean similarities between and within genera of the existing (not their proposed) classification, Clutton-Brock, Corbet, and Hills's data again show the proximity of *Dusicyon* to *Canis*. The mean intra-generic similarity of *Canis* is given as 83.9; the similarity between *Canis* and *Dusicyon* is 83.4. There are a number of inconsistencies in the conclusions drawn by these authors from their phenetic analysis, as can be seen by reconstruction of a portion of their table I entitled "Mean similarities between and within genera of the existing classification" (below).

According to these data, *Atelocynus* is not so close to *Dusicyon* as *Dusicyon* is to *Canis*, but Clutton-Brock, Corbet, and Hills have in-

cluded *Atelocynus* within the genus *Dusicyon*; they have not included *Dusicyon* within *Canis*. Some of the individual species, especially *Dusicyon australis*, *culpaeolus*, and *A. microtis* show a closer similarity to species of *Canis* (*adustus*, *mesomelas*, or *aureus*) than they do to other species placed in *Dusicyon*. Some idea of the subjectivity Clutton-Brock and colleagues employed in drawing their conclusions is evident in places in their text. For example, they suggested the inclusion of *D. australis* in *Canis* and of *Canis simensis*, *mesomelas*, and *adustus* in *Dusicyon* as a logical but ineffective means of distinguishing the two genera. They seemed to be making rather weak excuses for the maintenance of *Dusicyon* as a genus in face of their own data to the contrary.

An additional datum for the inclusion of *Dusicyon* in *Canis* was based on the report by Krieg (1925) of a case of hybridization between a South American canid called *Pseudalopex* and a domestic dog. The species involved was most likely *D. gymnocercus* (see Van Gelder, 1977), although others (Gray, 1972; Chiarelli, 1975) have listed it as *Cerdocyon thous*.

Too few data are available from the canids, especially the South American ones, for any conclusions to be drawn concerning their relationships on the basis of immunological or molecular studies (Seal, 1975). Similarly, the limited data from karyology offer no real help in establishing relationships. These have been summarized by Chiarelli (1975), who pointed out that there was a "close resemblance of the karyotypes of *Chrysocyon*, *Atelocynus*, *Dusicyon*, and *Speothos* with those of *Canis*."

On the basis of the various works cited above, especially that of Clutton-Brock, Corbet, and Hills (1976), the inclusion of a number of the species formerly called *Dusicyon* within the genus *Canis* is warranted. Langguth (1975) had already proposed this, and the phenetic

genus	<i>Canis</i>	<i>Dusicyon</i>	<i>Atelocynus</i>	<i>Cerdocyon</i>	<i>Chrysocyon</i>	<i>Speothos</i>
<i>Canis</i>	83.9					
<i>Dusicyon</i>	83.4	90.5				
<i>Atelocynus</i>	79.3	82.2	*			
<i>Cerdocyon</i>	79.4	84.8	86.1	*		
<i>Chrysocyon</i>	69.4	71.4	73.4	68.6	*	
<i>Speothos</i>	61.9	63.3	68.2	60.0	53.8	*

analysis of Clutton-Brock, Corbet, and Hills certainly suggests it, despite the reluctance by these investigators to propose it.

The decisions made by Clutton-Brock, Corbet, and Hills concerning *Dusicyon* and *Canis* may have been influenced by the extensive merger of species into the genus *Canis* that would result if they applied equally objective standards to the relationship of *Vulpes* to *Canis*. In this instance, however, no one had recently proposed the synonymizing of these two genera as Langguth had done for *Dusicyon* and *Canis*.

The genera *Alopex*, *Vulpes*, *Urocyon*, and *Fennecus* have been relatively stable for many years. Except for *Vulpes*, they are essentially monotypic genera. *Urocyon littoralis* is sometimes recognized as a valid species for the insular populations of *U. cinereoargenteus*, whereas others consider them as subspecies of *U. cinereoargenteus*. Clutton-Brock, Corbet, and Hills did not include *U. littoralis* in their analysis.

Alopex has been considered congeneric with *Vulpes*. Bobrinskii (1965) regarded it as a subgenus of *Vulpes*. Youngman (1975) also regarded the Arctic fox as a *Vulpes*. On the basis of the production of viable hybrids from crosses of *A. lagopus* and *V. vulpes*, I considered the two to be congeneric (Van Gelder, 1977). Clutton-Brock, Corbet, and Hills, however, found *Alopex* to be the most distinctive of the foxes and retained it as a genus.

The phenetic analysis of Clutton-Brock, Corbet, and Hills caused them to include *Fennecus* and *Urocyon* within the genus *Vulpes*. Here again, the data suggest that their conclusions were more subjective than objective. Below is an extract of their table of mean similarities between and within genera of the existing classification:

genus	<i>Vulpes</i>	<i>Dusicyon</i>	<i>Alopex</i>	<i>Fennecus</i>	<i>Urocyon</i>
<i>Vulpes</i>	86.9				
<i>Dusicyon</i>	86.0	90.5			
<i>Alopex</i>	79.2	79.0	*		
<i>Fennecus</i>	85.1	83.6	78.2	*	
<i>Urocyon</i>	85.0	84.5	74.4	82.5	*

These data show a high degree of similarity of both *Fennecus* and *Urocyon* to *Vulpes*. It

should be noted, however, that the similarity of *Dusicyon* to *Vulpes* is even greater, but Clutton-Brock, Corbet, and Hills did not seem to consider this to any great extent. In the lists of near neighbors for the various species of *Vulpes*, Clutton-Brock, Corbet, and Hills show that *Vulpes corsac*, *ferrilata*, *rueppelli*, *pallida*, *zerda*, and *chama* each have at least one species of *Dusicyon* more similar to each of them than some other members of the genus *Vulpes* are.

Clutton-Brock, Corbet, and Hills implied that their line of separation between genera is at the 80 percent level of similarity. From their table I of mean similarities, the level of 80 percent functions solely to separate *Alopex* from *Vulpes*. One wonders whether the 0.8 percent difference between 79.2 and 80.0 is of sufficient biological and taxonomic significance to warrant this. In their figure 5a (two-dimensional plot of Caninae using principal coordinates algorithm) the distance of *Alopex* from *Vulpes vulpes* seems less than *Atelocynus* or *Cerdocyon* are from the nearest *Dusicyon*. Clutton-Brock, Corbet, and Hills, as already mentioned, considered *Atelocynus* and *Cerdocyon* to be congeneric with *Dusicyon*. To me, the most significant data concerning the relationships of *Alopex* to *Vulpes* is the ability of the Arctic foxes to hybridize with *Vulpes vulpes* and to produce not only viable offspring, but fertile ones. *Alopex* has the highest number of chromosome arms of any of the canids, Fundamental Number, 88. *Vulpes vulpes* has 72. They have respectively, 25 and 18-20 pairs of somatic chromosomes (Chiarelli, 1975) but despite these differences, they are genetically compatible. I have discussed elsewhere (Van Gelder, 1977) the reasons why *Alopex* and *Vulpes* should be considered congeneric. Clutton-Brock, Corbet, and Hills stated that *Alopex* "lies close to the genus *Vulpes* but . . . it is the most aberrant of the foxes" as their reason for retaining it as a genus. Todd (1970) found no reason for recognizing *Alopex* as a genus.

The inclusion of *Fennecus* in *Vulpes* is more strongly founded, according to the phenetic analysis. *Fennecus* has a similarity to *Vulpes* even greater than that of *Alopex* to *Vulpes*, but as I have earlier mentioned, the similarity of

Dusicyon to *Vulpes* is still closer than that of *Fennecus*. The suggestion that *Fennecus* be incorporated in *Vulpes* does not seem to have been made before. Ellerman and Morrison-Scott (1951) stated that "Pocock did not retain it [*Fennecus*] as a genus, but there seems little doubt that it should be retained." I am, however, unable to find Pocock's statement to this effect in his 1941 work, the one presumably cited by Ellerman and Morrison-Scott. Clutton-Brock, Corbet, and Hills pointed out that *Fennecus* has nomenclatural priority over *Vulpes*, and Clutton-Brock and Corbet (1975) have applied to the International Commission of Zoological Nomenclature for a decision to maintain the name *Vulpes*.

Clutton-Brock, Corbet, and Hills's proposal to include *Urocyon* in *Vulpes* represented a change in the classification and nomenclature of genus that had been stable for nearly a century. They suggested that one of the reasons for the stability of *Urocyon* had been that no one had compared it with *Vulpes*, and that all attention to its affinities had been concerned with its possible relationship with *Dusicyon*. Their phenetic analysis showed that the five nearest neighbors of *Urocyon* are species of *Vulpes* (in order of proximity: *V. bengalensis*, *velox*, *corsac*, *rueppelli*, and *pallida*). The level of difference of *Urocyon* from these is about the same as *Vulpes zerda* is from its five nearest neighbors, and closer than *V. cana* or even *V. vulpes* is to its proximate species. From the phenetic data, it would seem that congeneracy between *Urocyon* and *Vulpes* is warranted, especially if *Fennecus* is also lumped with *Vulpes*. Similarly, if *Alopex* is congeneric with *Vulpes*, then both *Fennecus* and *Urocyon* are equally deserving of alliance in *Vulpes*. Todd (1970) found karyotypic similarity between *Urocyon* and *Fennecus*.

There is one report of hybridization between *Urocyon* and *Vulpes* (Bezdek, 1944). It is based on a furrier's skin, and there are no supporting data to reinforce its validity. However, if *Vulpes* and *Urocyon* are congeneric, somewhat more credence might be given to this report. Chromosomally, *Urocyon* has a Fundamental Number of 70 ($2n=66$). *Vulpes vulpes* has 72 chromosome arms ($2n=34-38$), and the other

species of *Vulpes* that have been reported (Chiarelli, 1975) also have a Fundamental Number of 72, but vary from 60 to 34 in their diploid number of chromosomes.

The final step in this analysis of the classification of the Canidae is the consideration of the relationship of *Vulpes* to *Canis* and *Vulpes* to *Dusicyon*. Clutton-Brock, Corbet, and Hills's figures of two-dimensional plots of the principal coordinates algorithm (figures 2a, 3a, 4a, and 5a) showed, generally, that while the traditional species of *Canis* seem separable from even the extended genus *Vulpes* (i.e., with *Fennecus*, *Urocyon*, and *Alopex*), *Dusicyon* fills an intermediate position and overlaps each of these.

The pertinent data on mean similarities between and within these three genera (excluding *Alopex*, *Fennecus*, *Urocyon*, *Atelocynus*, and *Cerdocyon*) are extracted from Clutton-Brock, Corbet, and Hills's table 1a:

genus	<i>Vulpes</i>	<i>Canis</i>	<i>Dusicyon</i>
<i>Vulpes</i>	86.9		
<i>Canis</i>	78.0	83.9	
<i>Dusicyon</i>	86.0	83.4	90.5

The similarity of *Dusicyon* to *Vulpes* is, from these data, almost the same as the similarity of the species of *Vulpes* are to their own generalized genus. The same is true for the similarity of *Dusicyon* to *Canis* relative to similarities of the species of *Canis* to their generalized genus.

Species of *Dusicyon* show up as one or more of the five nearest neighbors of species of *Vulpes* in more than 25 percent of the cases, whether *Fennecus*, *Urocyon*, or *Alopex* are included in *Vulpes* or not. *Canis* does not show up among the five closest relatives of any of the species of *Vulpes*, nor does any species of *Vulpes* appear as the nearest neighbor of any of the members of the genus *Canis* that Clutton-Brock, Corbet, and Hills analyzed. However, *Dusicyon* is represented as a nearest neighbor of species of *Canis* 45 percent of the time. Even if the bloodhound and dingo are excluded from this analysis as conspecific with *Canis lupus*, *Dusicyon* still represents more than 45 percent of the nearest neighbors. These data

serve to confirm the phenetic data that separate *Vulpes* and *Canis*, but which show a bridge between the two made by representatives of *Dusicyon*.

As Clutton-Brock, Corbet, and Hills put it, "No objective analysis of the results of this study would produce these three genera [*Canis/Vulpes/Dusicyon*] as presently composed." They noted that Langguth include a number of species of *Dusicyon* in *Canis* and they did not believe that his conclusions were "greatly at variance" with theirs. They stated, "if *Dusicyon* were merged with *Canis*, it would be difficult to argue that *Vulpes* should not be treated likewise."

Elsewhere (Van Gelder, 1977) I proposed the merger of both *Dusicyon* with *Canis*, following Langguth, and the joining of *Vulpes* with *Canis* as well. It was evidence from inter-

generic hybrids between *Dusicyon* and *Canis* and between *Vulpes* and *Canis* that led me to these conclusions and to analyze the other studies that were concerned with the relationships of these genera. Most students of both fossil and Recent canids acknowledge the similarities between these three genera, and, more than 30 years ago, Simpson (1945) stated, "Despite their world-wide distribution and an abundance of well-distinguished, more or less local species, the recent canines are quite uniform in structure, and it would be justified from many points of view to unite them all in a single genus."

Based on the analyses of Langguth (1975) for the South American canids, and those of Clutton-Brock, Corbet, and Hills (1976) for all the canids, the most appropriate current classification for the family seems to be:

Family Canidae

Genus *Canis* Linnaeus, 1758

Subgenus *Canis* Linnaeus, 1758

Canis (Canis) lupus Linnaeus, 1758

Canis (Canis) latrans Say, 1823

Canis (Canis) rufus Audubon and Bachman, 1851¹

Canis (Canis) familiaris Linnaeus, 1758²

Canis (Canis) aureus Linnaeus, 1758

Canis (Canis) adustus Sundevall, 1846

Canis (Canis) mesomelas Schreber, 1778

Canis (Canis) simensis Rüppell, 1835

Subgenus *Dusicyon* H. Smith, 1839

Canis (Dusicyon) australis Kerr, 1792

Subgenus *Pseudalopex* Burmeister, 1856

Canis (Pseudalopex) culpaeus Molina, 1782

Canis (Pseudalopex) gymnocercus (Fischer, 1814)

Canis (Pseudalopex) griseus Gray, 1837

Canis (Pseudalopex) sechurae Thomas, 1900

Subgenus *Lycalopex* Burmeister, 1854

Canis (Lycalopex) vetulus Lund, 1842

¹Clutton-Brock, Corbet, and Hills (1976), Stains (1975) and others used *Canis niger* Bartram, 1791, for the "red wolf." Bartram's names are on the Official Index of Rejected and Invalid Works in Zoological Nomenclature and the correct name for this species is *Canis rufus* Audubon and Bachman, 1851. See Nowak (1967), Paradiso (1968), and Paradiso and Nowak (1972) for comments. Its status as a species, hybrid population between *lupus* and *latrans*, or hybrid population between *lupus* and *familiaris* have been expressed (see McCarley, 1962, Nowak, 1970, Young and

Goldman, 1944, Lawrence and Bossert, 1967, Paradiso, 1968, and Paradiso and Nowak, 1972). Clutton-Brock, Corbet, and Hills did not include specimens of *Canis rufus* in their study.

²This name is commonly and universally applied to domestic dogs that are believed to have been domesticated from one or more subspecies of *Canis lupus*. What the status of domestic "species" should be in taxonomy is not resolved, and for the moment it seems best left alone.

- Subgenus *Cerdocyon* H. Smith, 1839
Canis (Cerdocyon) thous Linnaeus, 1766
 Subgenus *Atelocynus* Cabrera, 1940
Canis (Atelocynus) microtis Sclater, 1882
 Subgenus *Vulpes* Bowdich, 1821¹
Canis (Vulpes) vulpes Linnaeus, 1758
Canis (Vulpes) corsac Linnaeus, 1768
Canis (Vulpes) ferrilata (Hodgson, 1842)
Canis (Vulpes) bengalensis Shaw, 1800
Canis (Vulpes) cana (Blanford, 1877)
Canis (Vulpes) rueppelli Schinz, 1825
Canis (Vulpes) pallida Cretzschmar, 1826
Canis (Vulpes) zerda Zimmermann, 1780
Canis (Vulpes) chama A. Smith, 1833
Canis (Vulpes) velox Say, 1823
Canis (Vulpes) cinereoargenteus Schreber, 1775
Canis (Vulpes) littoralis (Baird, 1858)²
 Subgenus *Alopex* Kaup, 1829
Canis (Alopex) lagopus Linnaeus, 1758
 Genus *Nyctereutes* Temminck, 1839
Nyctereutes procyonoides (Gray, 1834)
 Genus *Chrysocyon* H. Smith, 1839
Chrysocyon brachyurus (Illiger, 1815)
 Genus *Speothos* Lund, 1839
Speothos venaticus (Lund, 1842)
 Genus *Cuon* Hodgson, 1838
Cuon alpinus (Pallas, 1811)
 Genus *Lycaon* Brookes, 1827
Lycaon pictus (Temminck, 1820)
 Genus *Otocyon* Müller, 1836
Otocyon megalotis (Desmarest, 1822)

Unfortunately, Clutton-Brock, Corbet, and Hills did not include *Canis (Canis) rufus* or (*Vulpes*) *littoralis* in their study. It is also regrettable that they did not list the catalogue numbers of the specimens that they utilized in their work. They seemed unaware that Langguth (1967) had demonstrated that both *Dusicyon culpaolus* and *D. inca* were based on mismatched skins and skulls of *D. culpaolus* and *D. gymnocercus*. It is impossible to ascertain how many specimens Clutton-Brock, Corbet, and Hills used in their analysis of *culpaolus* and *inca*, although it appears that only the holotypes were involved. However, the inclusion of these in their data-base as valid

species may well have biased some of their conclusions.

Elsewhere (Van Gelder, 1977), I have suggested that species capable of hybridizing should not be placed in separate subgenera. This suggestion was based on the same grounds as the reasons for not considering genera capable of hybridizing: that the upper level of the species involves reproductive incompatibility with other species. Of the canids on the preceding list, hybrids have been reported between the subgenera *Vulpes* and *Alopex*, between *Vul-*

¹For the use of *Vulpes* see Clutton-Brock and Corbet (1975) and Clutton-Brock, Corbet, and Hills (1976).

²Whether *Canis (Vulpes) littoralis* is a species closely allied to *C. (Vulpes) cinereoargenteus* or whether its populations are subspecies is largely a matter of opinion unsupported by any recent studies. Clutton-Brock, Corbet, and Hills (1976) did not include *littoralis* in their study.

pes and *Canis*, and between *Pseudalopex* and *Canis* (Gray, 1972; Van Gelder, 1977). An appropriate alternative would be to call each of the subgenera in the preceding list a "group," using the subgeneric name for each of them as in "*Vulpes*-group," or "*Canis*-group."

SUMMARY

Current studies of Recent canids seem to confirm a closer relationship between a number of species and groups of species than previously thought. The taxonomic conclusions presented in the publications of Clutton-Brock, Corbet, and Hills (1976) differ from those of Langguth (1975), and the present paper is an analysis of these classifications and an attempt to reconcile them. *Chrysocyon*, *Speothos*, *Nyctereutes*, *Cuon*, *Lycaon*, and *Otocyon* are regarded as monotypic genera, and the genus *Canis* is considered to be polytypic with eight subgenera or groups for the taxa formerly considered the genera *Dusicyon*, *Pseudalopex*, *Lycalopex*, *Cerdocyon*, *Atelocynus*, *Vulpes*, and *Alopex*.

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